

Comparative anatomy and significance of the sesamoid bone of the peroneus longus muscle (os peroneum)

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INTRODUCTION

An osseous structure, called a sesamoid bone or os peroneum, is occasionally found in man in the tendon of the peroneus longus muscle where it is angulated around the cuboid bone. The origin of the os peroneum has given rise to much controversy. Most authors find that this structure represents a response to the intense mechanical stresses involved in the angulated part of the tendon; thus the os peroneum is a classical and frequently used model for the origin of intratendinous ossifications due to mechanical stress. In contrast, other authors regard the os peroneum as a vestigial structure of phylogenetic significance. Studies of the os peroneum in man are numerous. This is not, however, the case for the other animal families; here the studies are rare and fragmentary with the exception of the work of Manners-Smith (1908) which is, however, purely descriptive and relates only to a limited number of observations.

The peroneus longus is similarly positioned in all pentadactyl mammals (Stieda, 1889; Frets, 1908; Edwards, 1928; Wildenauer & Muller, 1951; Welti, 1961; Jouffroy, 1971). It is part of the lateral group of leg muscles. The vertically positioned muscular belly is attached to the upper part of the lateral surface of the fibula and may, according to the species, extend up to the lateral epicondyle of the femur or to the lateral condyle of the tibia. In the middle part of the leg the muscular belly terminates as a long cylindrical tendon which continues the same vertical path as the muscle. At ankle level this tendon runs behind the lateral malleolus and then passes obliquely forwards across the lateral side of the calcaneus. At the lateral border of the foot the tendon bends almost through a right angle around the cuboid bone to reach the plantar surface of the foot. The sesamoid bone, when it is present, is situated in this angulated part of the tendon. The tendon then crosses the sole of the foot anteromedially to end mainly on the lateral tubercle of the base of the first metatarsal bone.

In non-human primates the peroneus longus is, in its role as an adductor of the hallux, of great importance in achieving a plantar grip. In the other eutherian mammals, the peroneus longus has no function in adduction of the hallux, and in man this function has disappeared due to the adductor attitude of the first digit. A comparative and systematic study of the anatomy of the os peroneum, bearing in mind the function of the peroneus longus, would therefore be of interest.

MATERIAL AND METHODS

The material used in the course of this work consisted of skeletons, bodies preserved in formalin, fresh cadavers and human radiographs.

Skeletons

174 primate skeletons were studied, subdivided as follows: LEMURIDAE: 11 *Lemur*, 2 *Lepilemur*, 3 *Hapalemur*; DAUBENTONIIDAE: 2 *Daubentonia*; INDRIDAE: 2 *Indri*, 3 *Propithecus*; CALLITHRICIDAE: 2 *Callithrix*; CEBIDAE: 2 *Alouatta*, 6 *Ateles*, 11 *Cebus*, 1 *Lagothrix*, 4 *Saimiri*; CERCOPITHECIDAE: 12 *Cercocebus*, 27 *Cercopithecus*, 1 *Colobus*, 1 *Cynopithecus*, 3 *Erythrocebus*, 40 *Macaca*, 31 *Papio*, 2 *Presbytis*, 1 *Pygathrix*, 3 *Theropithecus*; HYLOBATIDAE: 4 *Hylobates*. These skeletons belong to the collections from the Laboratoire d'Anatomie Comparée (Muséum National d'Histoire Naturelle, Paris) and from the Institut d'Anatomie Normale (Faculté de Médecine, Strasbourg).

The comparative material of non-primate pentadactyl mammals consisted of 100 skeletons representative of 19 genera belonging to 11 families: Order Carnivora: CANIDAE (*Canis*, *Vulpes*), FELIDAE (*Felis*), HYAENIDAE (*Hyaena*), MUSTELIDAE (*Lutra*, *Martes*, *Mustela*), URSIDAE (*Ursus*); Order Insectivora: ERINACEIDAE (*Erinaceus*), TALPIDAE (*Talpa*); Order Lagomorpha: LEPORIDAE (*Lepus*, *Oryctolagus*), Order Rodentia: CAVIIDAE (*Cavia*), GLIRIDAE (*Glis*), MURIDAE (*Apodemus*, *Cricetus*, *Microtus*, *Mus*, *Rattus*). These skeletons belong to the same collections as the primate skeletons. Since the peroneus longus is a motor muscle of the hallux, only the pentadactyl mammals were of real comparative interest.

Only skeletons dried with their ligaments and some of their tendons, in this case that of peroneus longus, were included; the sesamoid bones, being very small, are, in effect, often lost when the skeletons are too thoroughly cleaned, this frequently being the case in purely skeletal preparations.

A detailed macroscopic study of these skeletons was carried out.

Specimens preserved in formalin

The lower limbs of 15 adult primates were dissected: 2 *Lemur*, 1 *Daubentonia*, 2 *Cebus*, 1 *Cercocebus*, 1 *Cercopithecus*, 1 *Macaca*, 2 *Papio*, 1 *Hylobates concolor*, 1 *Gorilla*, 2 *Pan troglodytes*, 1 *Pongo pygmaeus*. All of these come from collections belonging to the Laboratoire d'Anatomie Comparée (Muséum National d'Histoire Naturelle, Paris).

In the case of the genera possessing the os peroneum as adults, the lower limbs of 4 young or stillborn subjects was also dissected: 1 *Cercocebus*, 2 *Macaca*, 1 *Papio*.

Fresh specimens

In the case of the non-human primates, 6 adult bodies were at our disposition: 2 *Lemur fulvus* (Institut d'Embryologie, Faculté de Médecine, Strasbourg), 1 *Macaca fascicularis* (Laboratoire de Psychophysiologie, U.L.P., Strasbourg), 1 *Hylobates concolor*, 1 *Pan troglodytes*, 1 *Pongo pygmaeus* (Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris).

20 human specimens, 11 male and 9 female, aged between 70 and 89 years, were studied during autopsies (Institut d'Anatomie Pathologique, Faculté de Médecine, Strasbourg).

In both fresh and preserved specimens the peroneus longus tendon was removed from both sides, examined under the binocular dissecting microscope, X-rayed and then fixed for a histological study. The radiographs were taken in the Service de Radiologie I (Hospices Civils, Strasbourg).

Table 1. *Personal observations in primates*

Family and Genus	Number of studied specimens	Number of specimens with os peroneum	Family and Genus	Number of studied specimens	Number of specimens with os peroneum
Lemuridae			Cercopithecidae		
<i>Lemur</i>	15	0	<i>Cercocebus</i>	13	13
<i>Lepilemur</i>	2	0	<i>Cercopithecus</i>	28	28
<i>Hapalemur</i>	3	0	<i>Colobus</i>	1	1
Daubentoniidae			<i>Cynopithecus</i>	1	1
<i>Daubentonia</i>	3	0	<i>Erythrocebus</i>	3	3
Indridae			<i>Macaca</i>	42	41
<i>Indri</i>	2	0	<i>Papio</i>	33	29
<i>Propithecus</i>	3	0	<i>Presbytis</i>	2	2
Callithricidae			<i>Pygathrix</i>	1	1
<i>Callithrix</i>	2	0	<i>Theropithecus</i>	3	3
Cebidae			Hylobatidae		
<i>Alouatta</i>	2	0	<i>Hylobates</i>	6	6
<i>Ateles</i>	6	0	Pongidae		
<i>Cebus</i>	13	0	<i>Gorilla</i>	1	0
<i>Lagothrix</i>	1	0	<i>Pan</i>	3	0
<i>Saimiri</i>	4	0	<i>Pongo</i>	2	0
			Hominidae		
			<i>Homo</i>	520	64

Human radiographs

500 radiographs of human feet (283 male and 217 female) were studied. These came from the archives of the Clinique Chirurgicale B (Hospices Civils, Strasbourg). They were taken during the surgical examination of adults aged between 20 and 60 years, with a mean age of 35 years. The feet were X-rayed both in dorsoplantar and in oblique projections. Radiographs showing pathological changes other than trauma were not included.

Histological techniques

The tendons were fixed in 5% formalin, decalcified in 10% hydrochloric acid (6–8 hours), dehydrated, cleaned in methyl benzoate followed by a toluene bath and embedded in paraffin. Longitudinal sections were cut at 10 μ m and stained with haemalum and eosin.

RESULTS

Non-primate pentadactyl mammals

From the hundred skeletons studied, we must conclude a total absence of the os peroneum in the non-primate pentadactyl mammals.

Prosimii

None of the Lemuridae, the Daubentoniidae nor the Indridae studied show an os peroneum.

Platyrrhini (New World monkeys)

None of the Callithricidae and the Cebidae studied show an os peroneum.



Fig. 1 (a-d). Radiographs of feet of Cercopithecidae showing the constant os peroneum (arrows) of this family. $\times 1$. (a) *Cercopithecus*. (b) *Macaca fascicularis*. (c) *Papio papio*. (d) *Presbytis* (*Semnopithecus*).

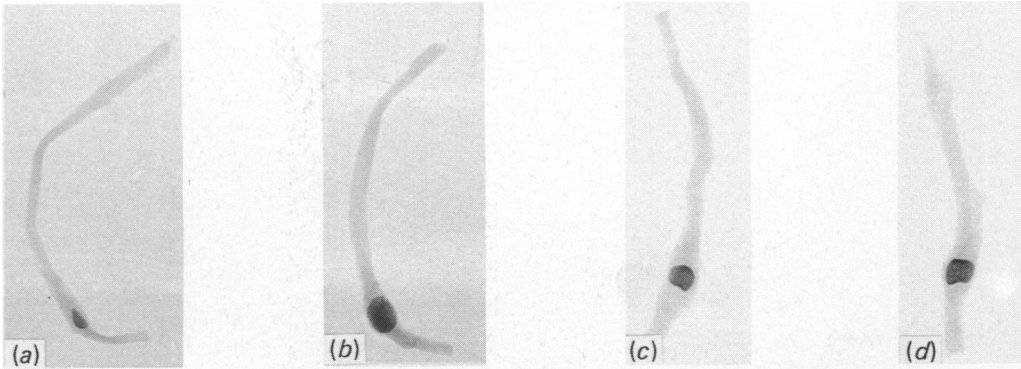


Fig. 2(a-d). Radiographs of peroneus longus tendons of Cercopithecidae and Hylobatidae showing the constant os peroneum of these families. $\times 1$. (a) *Cercopithecus nictitans*. (b) *Macaca irus*. (c, d) *Hylobates concolor*.

Catarrhini (Cercopithecidae, Old World monkeys)

In the Cercopithecidae, the os peroneum was observed in 122 cases out of 127 (96%), and always bilaterally (Table 1). In the five cases where it was missing, one belongs to the *Macaca* genus and the four others to the *Papio* genus.

The os peroneum in the Cercopithecidae is perfectly regular and similar in shape to a coffee bean (Figs. 1, 2a, b). Its position is constant at the level where the peroneus longus tendon bends onto the eminentia obliqua of the cuboid bone. The main axis of the os peroneum is directed obliquely downwards and anteromedially and is placed longitudinally in the tendon. The lateral surface of the bone is convex in all directions and non-articular; this surface is striated longitudinally due to the peripheral fibres of the tendon, and shows multiple vascular foramina. The medial surface forms a synovial joint with the corresponding facet of the cuboid bone; this surface is oval, smooth, flat or slightly concave and covered with hyaline cartilage.

The os peroneum is usually slightly larger than the sesamoid bones of the metatarsophalangeal joint of the hallux. Within the same genus, the size of the os peroneum varies with the size of the individual; the relative size varies according to the genus in question, the largest examples being found in the *Papio* genus, where dimensions can reach $15 \times 10 \times 7$ mm.

No examples of a congenital division of the os peroneum (os bipartitum or multipartitum), such as has been frequently described in man, were noted in the 244 bones, right and left, studied here.

The structure of the os peroneum in the adult Cercopithecidae is comparable to that of a typical short bone (Fig. 3c): a thin cover of compact bone surrounds a core of cancellous bone. The medial surface is covered with hyaline cartilage the architecture of which is identical to that of other articular cartilages, an area of calcified cartilage separating the cartilage from the bone. Chondroid cells, intermediate in type between fibrocytes and typical cartilaginous cells, are frequently observed between the collagenous bundles at the level of the tendinous attachment to the proximal and distal extremities of the sesamoid bone.

The histological study of the tendons of four newborn or young subjects of the Cercopithecidae family (two *Macaca* aged between 10 and 20 days, one *Cercocebus* aged 3 months and one *Papio* aged 2 years and 7 months) shows that the precursor of the os peroneum consists of a nodule of hyaline cartilage of the same form as that



Fig. 3(a-c). Histological structure and ossification of the os peroneum in Cercopithecidae. The medial surface of the tendon and the bone is above. $\times 20$. (a) Precursor of the os peroneum consisting of a nodule of hyaline cartilage in a *Cercocebus* aged 3 months. (b) Cartilaginous nodule in the process of ossifying in a young *Cercopithecus*. (c) Structure of the os peroneum in an adult *Macaca irus*.

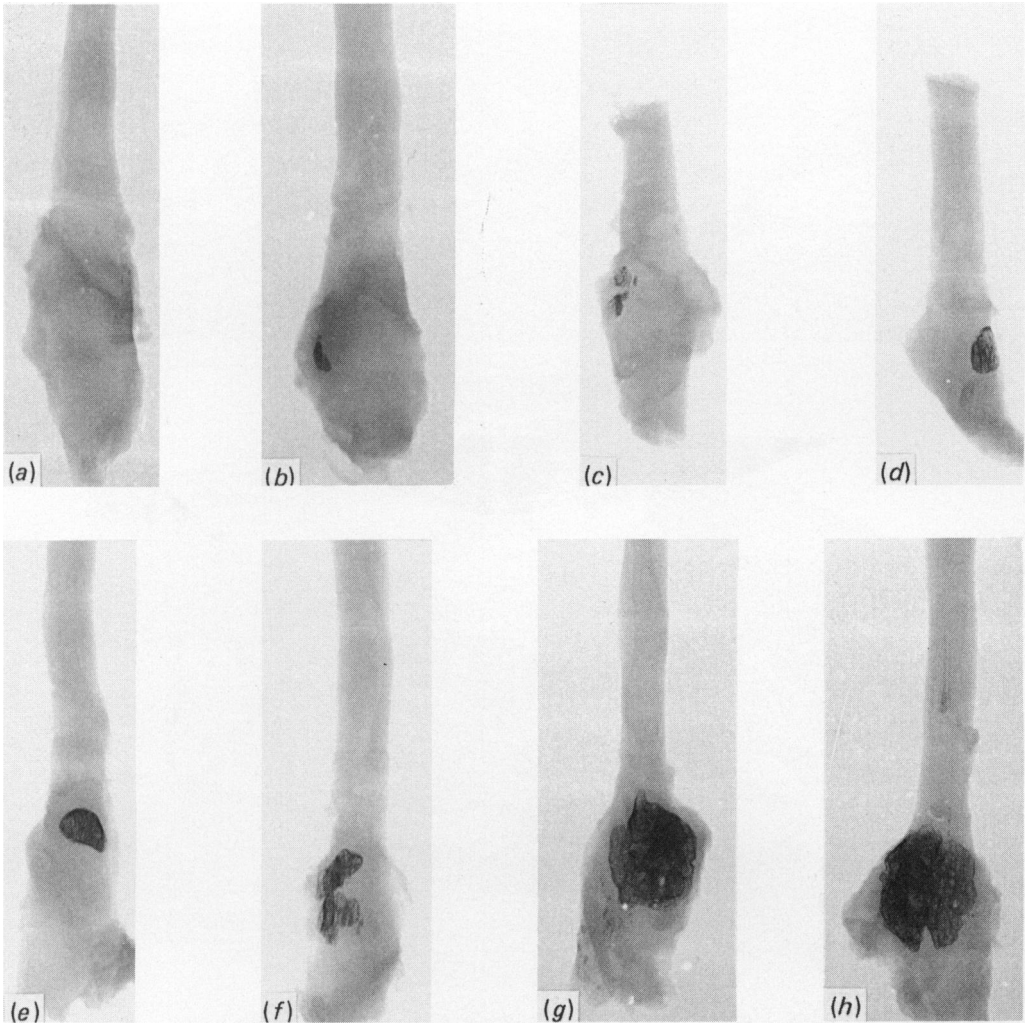


Fig. 4(a-h). Radiographs of human peroneus longus tendons showing the very variable shape of the os peroneum in Man. $\times 1$. (a) Absence of the os peroneum. (b-d) Small os peroneum eccentrically positioned in the tendon. (c) Small os peroneum bipartitum. (e) Regular os peroneum. (f) Os peroneum bipartitum. (g, h) Large os peroneum.

of the bone in the adult (Fig. 3a). In a young *Cercopithecus* this cartilaginous nodule was in the process of ossifying, the centre of ossification having already spread over two thirds of the structure (Fig. 3b). Thus the ossification of the os peroneum in the Cercopithecidae follows the typical endochondral pattern and is similar morphologically and chronologically to the ossification of all other short skeletal bones.

Hylobatidae

The os peroneum was observed on both sides in each of the five individuals studied (Table 1) which would seem to indicate a constant presence of this bone in the *Hylobates* genus.

The os peroneum of *Hylobates* is comparable in all respects to that of the Cercopithecidae (Fig. 2c, d); it is, however, a little smaller and its shape more elongated.

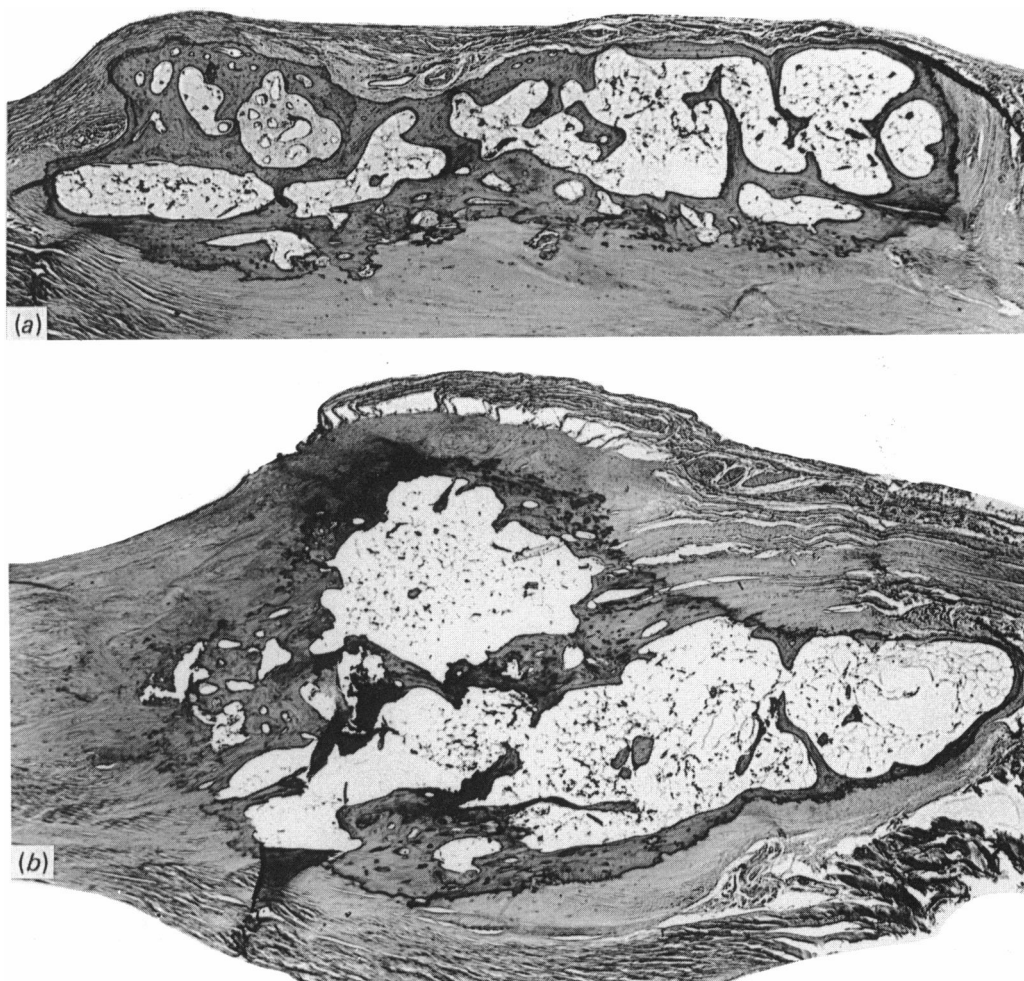


Fig. 5(a-b). Histological structure of the os peroneum in man.
The medial surface of the tendon is above. $\times 15$.

Pongidae

None of the *Pongidae* studied possessed an os peroneum.

Man

The os peroneum was found in 64 out of the 520 cases that were studied, a frequency of 12.3% (Table 1). Unlike the bone in the *Cercopithecidae*, the os peroneum in man is not always found bilaterally, and there is no difference in the frequency with which it is found on the two sides.

The shape of the os peroneum is very variable in man (Fig. 4). It can be either characteristic in its size and form (similar to the bone observed in the *Cercopithecidae*), or small but of characteristic form, or small and irregular. The os peroneum of man is frequently divided, without sign of any trauma, into two or more fragments (os bipartitum or multipartitum) (Fig. 4c, f).

The dimensions of the os peroneum are also very variable: the longitudinal

diameter varies between 2 and 13 mm with a mean of 7 mm. The size of the os peroneum is not related to the age of the subject; bones of small size can be found on very old subjects and bones of a large size on young subjects. The smaller examples of the os peroneum are usually eccentrically positioned in the tendon, being nearer to its anterior border (Fig. 4*b-d*).

The histological structure of the os peroneum in man is very variable as is the appearance of the bone in itself (Fig. 5). It can be a large nodule of cancellous bone surrounded by a thin layer of compact bone as in the Cercopithecidae, or merely a small osseous site composed of few trabeculae comparable with the structure of heterotopic ossifications. The surface of the tendon in contact with the cuboid bone is never formed of hyaline cartilage but always of typical tendinous tissue.

DISCUSSION

Distribution of the os peroneum in pentadactyl mammals

The complete absence of the os peroneum in the non-primate pentadactyl mammals is substantiated by the few reports in the literature (Pfitzner, 1892; Retterer & Lelièvre, 1911*b*; Forster, 1922*a*; Romankowowa, 1959; Wirtschafter & Tsujimura, 1961*a, b*). The absence of the os peroneum in the Prosimii is in accordance with the few observations of Manners-Smith (1908), Forster (1922*a*), Jouffroy (1962), and Wrobel (1966). In the Platyrrhini, the absence of the os peroneum is similarly noted by Manners-Smith (1908) and Forster (1922*a*).

The quasi-constant presence of the os peroneum in the Catarrhini is confirmed by the findings of Frets (1908), Retterer & Lelièvre (1911*b*), Forster (1922*a*), Weidenreich (1923), Ayer (1948) and Hartman & Straus (1961). In the framework of a study such as this, it is necessary to use only adult subjects where ossification is complete. Manners-Smith (1908) did not eliminate subjects which were too young and in some cases the cartilaginous outline of the os peroneum led him to erroneous conclusions.

The constant presence of the os peroneum in the Hylobatidae, more precisely in the *Hylobates* genus, is in accordance with the observations of Kohlbrugge (1891), Manners-Smith (1908) and Forster (1922*a*). There is still an absence of reports in the case of the *Symphalangus* genus.

For the Pongidae, the few anatomists who have explicitly looked for the os peroneum have noted its absence in *Gorilla* (Raven, 1950; Preuschoft, 1961), in *Pan troglodytes* (Sperino, 1897; Manners-Smith, 1908; Forster, 1922*a*; Meinel, 1971) and in *Pongo pygmaeus* (*Simia satyrus*) (Owen, 1830; Manners-Smith, 1908; Kohlbrugge & Retterer, 1912; Forster, 1922*a*; Boyer, 1935). Further work is necessary to determine whether the os peroneum is totally absent or only rare in the three Pongidae genera.

Much work has been done in investigating the os peroneum in man, either by anatomical and histological techniques (Gillette, 1872; Pfitzner, 1892, 1896; Parsons & Keith, 1897; Lunghetti, 1909; Weidenreich, 1923; Leutert, 1958) or, as in the majority of cases, by radiographic techniques (review in Siecke, 1964; Bogdanovic, Ilic, Mrvaljevic & Djordjevic-Camba, 1969). The frequency of the os peroneum in man has been estimated by authors (Siecke, 1964), their results varying between 2.3 and 22.9% of cases. Certain of these variations are due to the method used, for example, the very low values of less than 5% as recorded by certain authors are due to an inadequate radiological incidence, the visualisation of the os peroneum

Table 2. *Distribution of the os peroneum in pentadactyl mammals from personal observations and a review of the literature*

Group	Distribution of the os peroneum	Characters
Non-primate pentadactyl mammals	0	—
Prosimii	0	—
Platyrrhini (New World monkeys)	0	—
Catarrhini (Cercopithecidae, Old World monkeys)	Constant	Large and regular
Hylobatidae	Constant	Large and regular
Pongidae	Absent or rare	—
Man	20% (old subjects)	Most irregular

requiring an oblique projection. Low frequency values can also be explained if the specimens studied are too young and hence the growth of the os peroneum incomplete. Taking these young subjects into account would therefore tend to lower the apparent frequency of the os peroneum in comparison with that of older subjects, indeed the ossification of this bone in man seems late and its frequency increases until after the age of 50 years (Gillette, 1872; Fischer, 1912; Siecke, 1964). The maximum frequencies obtained from studies on old subjects are the most reliable and only the values from 18.3 to 22.9% (Parsons & Keith, 1897; Lunghetti, 1909; Fischer, 1912; Siecke, 1964) will be used here to compare with other animal families. The attempts to prove a sexual difference in the frequency of the os peroneum (Pfitzner, 1892, 1896; Parsons & Keith, 1897; Siecke, 1964) are not conclusive and hence it can be stated that the frequencies are close if not equal for the two sexes.

From our own observations and a review of the literature, it appears that the os peroneum is distributed over only a few primate families (Table 2). This bone is constant, large and regular in the Cercopithecidae (Catarrhini, Old World monkeys) and the Hylobatidae. On the contrary the os peroneum seems to be completely absent in the non-primate pentadactyl mammals, in the Prosimii and in the Platyrrhini (Old World monkeys). The os peroneum is absent or rare in the Pongidae and relatively infrequent in man.

Classical theories concerning the origin of the os peroneum

The origin and the significance of the os peroneum, as for all other sesamoid bones, are very controversial. The numerous interpretations can be grouped under two main and totally opposing theories: the theory of individual mechanical differentiation and the phylogenetic theory.

The theory of individual mechanical differentiation of the os peroneum is upheld by the majority of authors (Gillette, 1872; Lunghetti, 1909; Retterer & Lelièvre, 1911*a*, 1912*a, b*; Kohlbrugge & Retterer, 1912; Forster, 1922*a*; Anthony, 1923; Weidenreich, 1923; Leutert, 1958; Meyer, Sick & Grosshans, 1964; Siecke, 1964) and is adopted in the classical treatises of general and pathological anatomy and of functional histology (Souteyrand-Boulenger, 1971; Knese, 1979). According to this theory, the os peroneum appears in the tendinous tissue in reaction to the unusual mechanical stresses occurring in the area where the peroneus longus tendon bends around the cuboid bone. The precise nature of these unusual stresses varies according

to the author. This theory developed as a result of work on the functional adaptation of tendons subject to mechanical stresses in the more general study of the relations between the differentiation of structured connective tissues and mechanical stresses (Lunghetti, 1909; Retterer & Lelièvre, 1911 *a, b*, 1912 *a, b*; Weidenreich, 1923; Ploetz, 1938; Pauwels, 1940, 1960; Leutert, 1955; Altmann, 1964; Sick, 1964; Meyer, Sick & Grosshans, 1964). From the evidence gathered in the cases of the Cercopithecidae and the Hylobatidae of an *os peroneum* that is constant, large and regular, and with a histological structure and mode of ossification identical to that of other short bones of the skeleton, this theory of individual mechanical differentiation is not favoured, at least not in these families.

The phylogenetic theory is the main opposing theory to the one stated above. The *os peroneum* is considered as the phylogenetical remnant of a primitive supplementary bone, or as an additional digital ray ('postminimus'), or as a separated muscular tubercle. The theory of 'traction epiphysis' or 'Abgliederungstheorie' (Pfitzner, 1892, 1896; Pearson & Davin, 1921) suggests that the sesamoid bones are muscular tubercles or insertion tuberosities that have become secondarily disconnected and thus free under the effect of muscular traction, as for instance the sesamoid bone of the tibialis posterior (*os tibiale externum*, accessory navicular) and the medial tuberosity of the navicular. Other examples are the sesamoid bone of the quadriceps femoris (patella) and the olecranon. But Pfitzner (1892, 1896) himself has emphasised the difficulties of applying this theory to the *os peroneum*. The study of comparative anatomy does not support the traction epiphysis theory for the origin of the *os peroneum* since no tuberosity with the potential of separation under muscular traction exists in any mammalian family lacking an *os peroneum*.

In contrast to the above theories is the concept of Drexler (1958) who thought that the presence of the *os peroneum* in man was related to the existence of unusual tendinous insertions. These additional insertions are, in fact, often found even in the absence of the *os peroneum* and have previously been described (Le Double, 1897); furthermore this theory does not explain the existence of an *os peroneum* in non-human primates.

It is therefore necessary to reconsider the significance of the *os peroneum* in the Cercopithecidae and the Hylobatidae independently from that in man.

Significance of the os peroneum in the Cercopithecidae and the Hylobatidae

The *os peroneum* of the Cercopithecidae and the Hylobatidae is an instance of a new skeletal element added to the fundamental tetrapod skeleton. This osseous structure, which appeared in a tendon subject to unusual mechanical stresses, became genetically fixed and thus hereditarily transmitted. This manner of its appearance is analogous to that accepted for the origin of the patella in the quadriceps femoris tendon (Vallois, 1917; Lessertisseur & Saban, 1967) and for the origin of many other tenotogenous sesamoid bones (Parsons, 1904, 1908; Haines, 1940; Barnett & Lewis, 1958).

It is interesting to try to define the conditions necessary for the formation of the *os peroneum*, which must be correlated with the statics and dynamics of the foot in the primates; this has been exhaustively studied (Weidenreich, 1922; Forster, 1922 *a, b*, 1923, 1924; Hafferl, 1929, 1933; Welti, 1961; Lamy, 1983). The mechanical factors concomitant with the appearance of an osseous structure in the angulated region of the peroneus longus tendon are seemingly linked to the functional importance of this muscle in the adduction and pseudo-opposability of the hallux in

the non-human primates which gives rise to repeated friction of the tendon on the cuboid bone. The variation in locomotory behaviour, associated with this role of the peroneus longus in the prehensility of the first digit – vertical clinging and leaping (*Lemur*, *Lepilemur*, *Hapalemur*, *Propithecus*), quadrupedal terrestrial and semi-terrestrial walking and running (*Cercopithecus*, *Papio*, etc.), hanging and swinging (*Hylobates*, etc.), bipedal walking and running – are not sufficient to explain the total absence of the os peroneum in the Prosimii and in the Platyrrhini (New World monkeys), and its constant presence in the Catarrhini (*Cercopithecidae*, Old World monkeys) and in the Hylobatidae; to explain this distribution it is necessary to invoke the genetic factors previously mentioned.

Significance of the os peroneum in man

In man, the os peroneum may be interpreted as a regressive form of that bone constantly found in the *Cercopithecidae* and in the *Hylobatidae*. Many arguments exist favouring the idea that the human ossicle is regressive. The existence of very variable forms supports this concept, as does its frequent absence.

The significance of the presence in man of an os peroneum bipartitum or multipartitum (approximately 30 % of the bones, Burman & Lapidus, 1931; Siecke, 1964), a phenomenon seemingly not found in the Catarrhini, has been widely discussed. For certain authors these fragmented forms, which must not be confused with the very rare cases noted of real fractures (Mains & Sullivan, 1973), are the consequence of repetitive minor injuries. For other authors, these fragmented forms are, on the contrary, of congenital origin and are due to multiple centres of ossification, associated with the regression of the os peroneum (Pfitzner, 1892, 1896; Burman & Lapidus, 1931). The same phenomenon of fragmentation is found in other human sesamoid bones like those of the metatarsophalangeal joint of the hallux (Le Minor, 1984) or the patella (Wütschke, 1966).

The existence of unilateral cases of the os peroneum in man (approximately 40 % of cases, Pfitzner, 1896; Siecke, 1964) is in total contrast to the invariable bilateral occurrence in the Catarrhini and can also be attributed to the regressive nature of this bone. The unilateral presence of an anatomical structure is often found in the case of a regressive form, for example the palmaris longus muscle which is regressive in man and can be absent unilaterally or bilaterally.

The seemingly tardy ossification of the os peroneum observed in man (Gillette, 1872; Fischer, 1912; Siecke, 1964) has been interpreted by certain authors as a proof of the mechanical origin of the bone, but this delay is comparable to that established for the os trigonum (located at the level of the lateral tubercle of the talus), or for the fabella (Fischer, 1912). In the case of the os peroneum in man, this late ossification could be linked to its regression since regressive structures which have lost their functional importance generally ossify later.

It is interesting to note that a parallel evolution to that which has been observed for the os peroneum is happening to other sesamoid bones constantly present in the Catarrhini and apparently regressive and in the act of disappearing in man: metacarpo- and metatarsophalangeal sesamoid bones, the radial sesamoid bone at the insertion of the abductor pollicis longus, the posterior sesamoid bones of the knee (medial and lateral fabellae in the gastrocnemius muscle, the cyamella in the popliteus) and the sesamoid bone at the base of the fifth metatarsal.

Associated with the regression of the os peroneum in man, another factor, besides that of a fundamental genetic nature, is the disappearance of the repetitive friction

of the peroneus longus tendon on the cuboid bone. This friction, replaced by a permanent compression, disappears with the loss of the hallux opposability and its alignment with the other digits, concomitant with the acquisition of erect posture and bipedal walk (Lazarus, 1896; Weidenreich, 1922; Forster, 1922*a, b*, 1923, 1924; Hafferl, 1929, 1933; Welti, 1961; Lamy, 1983).

SUMMARY

The os peroneum is found in only a few primate families and seems to be completely absent in the non-primate pentadactyl mammals, in the Prosimii and in the Platyrrhini (New World monkeys).

In the Cercopithecidae (Catarrhini, Old World monkeys) and the Hylobatidae, the os peroneum is a coffee bean-shaped constant, large and regular bone. The lateral surface of the bone is convex in all directions and non-articular. The medial surface is covered with hyaline cartilage and articulates by means of a synovial joint with the corresponding facet of the cuboid bone. The histological structure and the mode of ossification of the os peroneum are identical to that of other short bones of the skeleton. The os peroneum of the Cercopithecidae and Hylobatidae is an example of a new skeletal element that has appeared in a tendon subject to unusual mechanical stress. In the case of the peroneus longus tendon the stress is due to repetitive friction because of the functional importance of this muscle in the adduction and pseudo-opposability of the hallux. This osseous element is genetically fixed and hereditarily transmitted. Its mode of appearance is analogous to that accepted for the origin of the patella.

In the Pongidae, the os peroneum is absent or rare. In man, this bone is relatively infrequent (approx 20% of mature individuals) and its shape is most irregular. In this case, the os peroneum appears as a regressive form of the typical bone observed in the above families, which is in the process of disappearing. Besides fundamental genetical factors, this regression is probably in relation to the disappearance of the functional importance of the peroneus longus muscle to the loss of the hallux opposability. Thus the mechanical factors cannot be dissociated from the genetic and phylogenetic factors in explaining the appearance and the regression of the os peroneum.

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REFERENCES

- ALTMANN, K. (1964). Zur kausalen Histogenese des Knorpels. *Ergebnisse der Anatomie und Entwicklungsgeschichte* 37, 1-130.
- ANTHONY, R. (1923). *Le Déterminisme et l'Adaptation Morphologiques en Biologie Animale*, p. 314. Paris: Doin.
- AYER, A. A. (1948). *The Anatomy of Semnopithecus entellus*, p. 33. Madras: Indian Publishing House.
- BARNETT, C. H. & LEWIS, O. J. (1958). The evolution of some traction epiphyses in birds and mammals. *Journal of Anatomy* 92, 593-601.

- BOGDANOVIC, D., ILIC, A., MRVALJEVIC, D. & DJORDJEVIC-CAMBA, V. (1969). Les osselets surnuméraires du tarse humain les plus fréquents et leur importance clinique. Recherches radiologiques et vérifications anatomiques. *Comptes rendus de l'Association des anatomistes* **54**, 421-429.
- BOYER, E. L. (1935). The musculature of the inferior extremity of the orang-utan *Simia satyrus*. *American Journal of Anatomy* **56**, 193-256.
- BURMAN, M. S. & LAPIDUS, P. W. (1931). The functional disturbances caused by the inconstant bones and sesamoids of the foot. *Archives of Surgery* **22**, 936-975.
- DREXLER, L. (1958). Fixation der Sehne der M. peroneus longus und Os peroneum. *Acta anatomica* **35**, 345-346.
- EDWARDS, M. E. (1928). The relations of the peroneal tendons to the fibula, calcaneus and cuboideum. *American Journal of Anatomy* **42**, 213-253.
- FISCHER, H. (1912). Beitrag zur Kenntnis der Skelettvarietäten (überzählige Karpalia und Tarsalia, Sesambeine, Kompaktinseln). *Fortschritte auf dem Gebiete der Röntgenstrahlen* **19**, 43-66.
- FORSTER, A. (1922a). La voûte tarsienne transversale, sa formation et son mécanisme. *Archives de morphologie générale et expérimentale* **6**, 1-188.
- FORSTER, A. (1922b). Contribution à la formation du gros orteil dans l'espèce humaine. *Archives d'anatomie, d'histologie et d'embryologie* **1**, 279-290.
- FORSTER, A. (1923). La première articulation cunéo-métatarsienne chez les mammifères supérieurs: Prosimiens et Primates. *Archives d'anatomie, d'histologie et d'embryologie* **2**, 395-428.
- FORSTER, A. (1924). Etude sur l'évolution du pied humain, la voûte longitudinale. *Archives d'anatomie, d'histologie et d'embryologie* **3**, 195-246.
- FRETS, G. P. (1908). Die Varietäten der Musculi peronei beim Menschen und die Mm. peronei bei den Säugetieren. *Morphologisches Jahrbuch* **38**, 135-193.
- GILLETTE (1872). Des os sésamoïdes chez l'homme. *Journal de l'anatomie et de la physiologie* **8**, 506-538.
- HAFFERL, A. (1929). Bau und Funktion des Affenfusses. Ein Beitrag zur Gelenk- und Muskelmechanik: die Anthropoiden. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **88**, 749-783.
- HAFFERL, A. (1933). Bau und Funktion des Affenfusses. Ein Beitrag zur Gelenk- und Muskelmechanik: die Prosimien. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **99**, 63-112.
- HAINES, R. W. (1940). Note on the independence of sesamoid and epiphyseal centres of ossification. *Journal of Anatomy* **74**, 101-105.
- HARTMAN, C. G. & STRAUS, W. L. (1961). *The Anatomy of Rhesus Monkey (Macaca mulatta)*, 2nd ed., p. 164. New York: Hafner.
- JOUFFROY, F. K. (1962). La musculature des membres chez les Lémuriens de Madagascar. *Mammalia* **26**, Suppl. 2, 216-217.
- JOUFFROY, F. K. (1971). Musculature des membres. In *Traité de Zoologie* (ed. P. P. Grassé), T. 16, Fasc. 3, pp. 1-475. Paris: Masson.
- KNESE, K. H. (1979). *Stützgewebe und Skelettsystem*, pp. 463-466. Berlin: Springer.
- KOHLBRUGGE, J. H. F. (1891). Versuch einer Anatomie des Genus Hylobates. In *Zoologische Ergebnisse einer Reise in Niederländisch-Ost Indien* (ed. M. Weber), vol. 1, pp. 211-354.
- KOHLBRUGGE, J. H. F. & RETTERER, E. (1912). Du pied et du long péronier latéral d'un orang-outang adulte. *Comptes rendus de la Société de biologie* **72**, 256-257.
- LAMY, P. (1983). Le système podal de certains hominidés fossiles du pliopleistocène de l'Afrique de l'Est: étude morpho-dynamique. *L'Anthropologie* **87**, 435-464.
- LAZARUS, S. P. (1896). Zur Morphologie des Fuss skelettes. *Morphologisches Jahrbuch* **24**, 1-166.
- LE DOUBLE, A. F. (1897). *Traité des Variations du Système Musculaire de l'Homme*, pp. 334-335. Paris: Schleicher.
- LE MINOR, J. M. (1984). Sésamoïdes bipartita du gros orteil. *Radiologie* **4**, 169-172.
- LESSERTISSEUR, J. & SABAN, R. (1967). Squelette appendiculaire. In *Traité de Zoologie* (ed. P. P. Grassé), T. 16, Fasc. 1, pp. 709-1078. Paris: Masson.
- LEUTERT, G. (1955). Über den Bau der Sehne des M. fibularis longus im Bereich des äusseren Fussrandes. *Zeitschrift für mikroskopisch-anatomische Forschung* **61**, 512-532.
- LEUTERT, G. (1958). Über den histologischen Aufbau des Os peroneum. *Zeitschrift für mikroskopisch-anatomische Forschung* **64**, 639-651.
- LUNGHEtti, B. (1909). Contributo allo studio della morfologia e dello sviluppo dei sesamoidi intratendinei. *Internationale Monatsschrift für Anatomie und Physiologie* **26**, 47-82.
- MAINS, D. B. & SULLIVAN, R. C. (1973). Fracture of the Os peroneum. *Journal of Bone and Joint Surgery* **55A**, 1529-1530.
- MANNERS-SMITH, T. (1908). A study of the cuboid and os peroneum in the primate foot. *Journal of Anatomy* **42**, 397-414.
- MEINEL, W. (1971). Vergleichend anatomische Untersuchungen an der Fuss und Unterschenkelmuskulatur des Schimpansen. *Zoologische Beiträge* **17**, 227-305.
- MEYER, P., SICK, H. & GROSSHANS, E. (1964). Adaptation fonctionnelle au glissement et à la réflexion des tendons, des poulies de réflexion des tendons et des ligaments articulaires. *Archives de biologie* **75**, 745-770.

- OWEN, R. (1830). On the anatomy of the Orang-Utang. *Proceedings of the Zoological Society of London*, 67–72.
- PARSONS, F. G. (1904). Observations on traction epiphyses. *Journal of Anatomy* 38, 248–258.
- PARSONS, F. G. (1908). Further remarks on traction epiphyses. *Journal of Anatomy* 42, 388–395.
- PARSONS, F. G. & KEITH, A. (1897). Seventh report of the Committee of collective investigation of the Anatomical Society of Great Britain and Ireland for the year 1896–97. *Journal of Anatomy* 32, 182–186.
- PAUWELS, F. (1940). Grundriss einer Biomechanik des Frakturheilung. *Verhandlungen der deutschen orthopaedischen Gesellschaft* 34, 62–108.
- PAUWELS, F. (1960). Eine neue Theorie über den Einfluss mechanischer Reize auf die Differenzierung der Stützgewebe. *Zeitschrift für Anatomie und Entwicklungsgeschichte* 121, 478–515.
- PEARSON, K. & DAVIN, A. G. (1921). On the sesamoids of the knee joint. *Biometrika* 13, 133–175 and 350–400.
- PFITZNER, W. (1892). Die Sesambeine des menschlichen Körpers. *Morphologische Arbeiten (Schwalbe)* 4, 517–762.
- PFITZNER, W. (1896). Die Variationen im Aufbau des Fuss skelets. *Morphologische Arbeiten (Schwalbe)* 6, 245–527.
- PLOETZ, E. (1938). Funktioneller Bau und funktionelle Anpassung der Gleitsehnen. *Zeitschrift für Orthopaedie und ihre Grenzgebiete* 67, 212–234.
- PREUSCHOTT, H. (1961). Muskeln und Gelenke der Hinterextremität des Gorilla. *Morphologisches Jahrbuch* 101, 432–540.
- RAVEN, H. C. (1950). *The Anatomy of the Gorilla*, p. 65. New York: Colombia University Press.
- REITTERER, E. & LELIÈVRE, A. (1911a). Des sésamoides vésiculo-fibreux des mammifères. *Comptes rendus de la Société de biologie* 71, 5–8.
- REITTERER, E. & LELIÈVRE, A. (1911b). Mécanomorphose des tissus de substance conjonctive. *Comptes rendus de la Société de biologie* 71, 312–315.
- REITTERER, E. & LELIÈVRE, A. (1912a). Du tendon réfléchi du long péronier latéral du Chimpanzé. *Comptes rendus de la Société de biologie* 72, 154–156.
- REITTERER, E. & LELIÈVRE, A. (1912b). Du pied et du tendon du long péronier latéral d'un jeune orang-outang. *Comptes rendus de la Société de biologie* 72, 237–240.
- ROMANKOWOWA, A. (1959). The sesamoid bones of the autopodia of Insectivora and Rodentia. *Zoologica poloniae* 10, 225–256.
- SICK, H. (1964). L'adaptation des tendons à la réflexion. *Archives d'anatomie, d'histologie et d'embryologie* 47, 370–446.
- SIECKE, H. (1964). Beitrag zur Genese des Os peroneum (Beobachtungen an 250 röntgenologisch festgestellten Ossa peronea). *Zeitschrift für Orthopaedie und ihre Grenzgebiete* 98, 358–370.
- SOUTEYRAND-BOULENGER, J. D. (1971). Arthrologie. In *Traité de Zoologie* (ed. P. P. Grassé), T. 16, Fasc. 3, pp. 837–1157. Paris: Masson.
- SPERINO, G. (1897). *Anatomia del Cimpanze*. Torino: Unione tipogr.
- STIEDA, L. (1889). Der M. peroneus longus und die Fussknochen. *Anatomischer Anzeiger* 4, 600–607; 624–640; 652–661.
- VALLOIS, H. (1917). La valeur morphologique de la rotule chez les Mammifères. *L'Anthropologie. Bulletin de la Société anthropologique de Paris* 8, 1–33.
- WEIDENREICH, F. (1922). Der Menschenfuss. *Zeitschrift für Morphologie und Anthropologie* 22, 51–282.
- WEIDENREICH, F. (1923). Knochenstudien. Über Sehnenverknöcherungen und Faktoren der Knochenbildung. *Zeitschrift für Anatomie und Entwicklungsgeschichte* 69, 558–597.
- WELTI, H. (1961). Contribution à l'étude de la morphologie et de la fonction des muscles jambier antérieur et long péronier latéral. *Archives d'anatomie, d'histologie et d'embryologie* 44, 61–100.
- WILDENAUER, E. & MULLER, W. (1951). Die Sehne des M. fibularis longus im Bereich des Os cuboides und ihre Beziehungen zu den kurzen Fussmuskeln. *Zeitschrift für Anatomie und Entwicklungsgeschichte* 115, 443–451.
- WIRTSCHAFTER, Z. T. & TSUJIMURA, J. K. (1961a). The sesamoid bones in the C3H mouse. *Anatomical Record* 139, 399–408.
- WIRTSCHAFTER, Z. T. & TSUJIMURA, J. K. (1961b). The sesamoid bones in Long-Evans strain rats. *Anatomical Record* 141, 195–204.
- WROBEL, K. H. (1966). Funktionelle Anpassungserscheinungen der Muskulatur des Lorisidenfusses. *Morphologisches Jahrbuch* 109, 448–469.
- WUTSCHKE, J. (1966). Patella partita und Patella duplex. *Fortschritte auf dem Gebiete der Roentgenstrahlen und der Nuklearmedizin* 104, 260–266.